

Lobopodia



Complete fossil of *Aysheaia pedunculata*, showing overall morphology.

The **lobopodians**, members of the informal group **Lobopodia**^[2] (from the Greek, meaning "blunt feet"), or the formally erected phylum **Lobopoda** Cavalier-Smith (1998),^[3] are panarthropods with stubby legs called **lobopods**,^[4] a term which may also be used as a common name of this group as well.^{[5][6]} While the definition of lobopodians may differ between literatures, it usually refers to a group of soft-bodied, worm-like fossil panarthropods such as *Aysheaia* and *Hallucigenia*.^[4]

The oldest near-complete fossil lobopodians date to the Lower Cambrian; some are also known from Ordovician, Silurian and Carboniferous Lagerstätten.^{[7][8][9]} Some bear toughened claws, plates or spines, which are commonly preserved as carbonaceous or mineralized microfossils in Cambrian strata.^{[10][11]}

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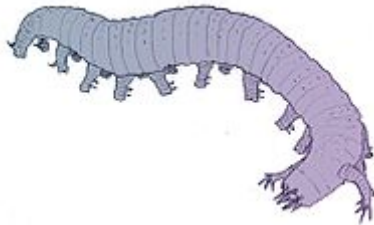
Lobopodia

Temporal range:

Cambrian Series 2–Early Pennsylvanian^[1]

PreЄ **Є** **O** **S** **D** **C** **P** **T** **J** **K** **PgN**

The taxa Onychophora, Tardigrada, and Euarthropoda survive to Recent



Reconstruction of the lobopodian *Aysheaia pedunculata*

Scientific classification

Kingdom: Animalia

(unranked): Panarthropoda

Phylum: †**"Lobopodia"**
Snodgrass 1938

Groups included

- † "Xenusia"
- † *Pambdelurion* and † *Kerygmachela* (excluded in some usages)
- Onychophora (in some usages)
- Tardigrada (in some usages)
- Arthropoda (in some usages)

Cladistically included but

As stem-group onychophorans As stem-group tardigrades As stem-group panarthropods	traditionally excluded taxa
Described genera	Crown-group Euarthropoda
References	Synonyms
	Lobopoda Cavalier-Smith (1998)

Definition

The scope of the Lobopodian concept varies from author to author. Its most general as well as the most limited sense refers to a suite of mainly Cambrian worm-like panarthropod taxa with lobopods – for example *Aysheaia*, *Hallucigenia* and *Xenusion*, members which were traditionally united as "xenusians" or "xenusiids" (class *Xenusia*). The dinocaridid genera *Pambdelurion* and *Kerygmachela* may also be regarded as lobopodians,^{[12][13]} eventually referred as "gilled lobopodians" or "gilled lobopod".^[14] Under such definitions, "Lobopodia" compose of only extinct taxa, and widely accepted as an informal, paraphyletic grade in correspond to the crown-group of three extant panarthropod phyla: Onychophora (velvet worms), Tardigrada (waterbears) and Arthropoda (arthropods).^{[4][15][16][17][18][19]}

An alternative, broader definition of lobopodians would also incorporate the extant phyla Onychophora and Tardigrada,^{[20][12][3]} two groups of panarthropod which also bore lobopodous limbs as well.^[4] "Lobopodia" may also refer to a possible clade sister to Arthropoda, and compose of only Tardigrada and Onychophora.^[21] The broadest definition proposes the monophyletic superphylum Lobopodia is equivalent to Panarthropoda.^{[22][5]}

Representative taxa

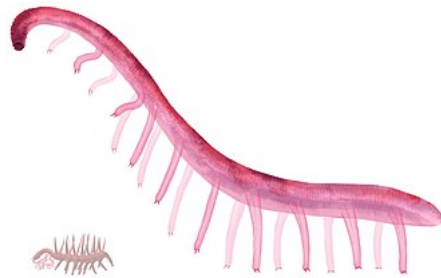


Aysheaia pedunculata and *Hallucigenia sparsa*, two of the most iconic as well as the first described^[4] lobopodians.

The better-known genera include, for example, *Aysheaia*, which was discovered in the Canadian Burgess Shale and *Hallucigenia*, known from both Chenjiang Maotianshan Shale and the Burgess Shale. *Aysheaia pedunculata* has morphology apparently basic for lobopodians^[15] — for example significantly annulated cuticle, terminal mouth opening, specialized frontalmost appendages and stubby lobopods with terminal claws. *Hallucigenia sparsa* is famous by having a complex history of interpretation — it was originally reconstructed with long, stilt-like legs and mysterious fleshy dorsal protuberances, and was long considered a prime example of the way in which nature experimented with the most diverse and bizarre body designs during the Cambrian.^[23] However, further discoveries showed that this reconstruction had placed the animal upside-down: interpreting the "stilts" as dorsal spines made it clear that the fleshy "dorsal" protuberances were actually elongated lobopods. More recent reconstruction even exchanged the front and rear ends of the animal: reveal the bulbous inprint previously thought to be a head was actually gut contents being expelled from its anus.^{[10][16]}

Microdictyon is another charismatic as well as the speciose genus of lobopodians resembling *Hallucigenia*, but instead of spines, it bore pairs of net-like plates which often found disarticulated and known as an example of small shelly fossils (SSF). *Xenusion* has the oldest fossil record amongst described lobopodians which may trace back to Cambrian Stage 2.^{[20][13]} *Luolishania* is an iconic example of lobopodians with multiple pairs of specialized appendages.^[24] The gill lobopodians *Kerygmachela* and *Pambdelurion* shed light on the relationship between lobopodians and arthropods, as they have both lobopodian affinities and characters link to the arthropod stem-group.^{[14][22]}

Morphology



Paucipodia inermis (right) and *Hallucigenia sparsa* (bottom left) in scale. Fossils of *Xenusion*, a lobopodian that may have grown up to 20 centimeters.

Most lobopodians are only a few centimeters in length, while some genera may have grown up to over 20 centimeters.^[6] Their bodies are annulated, although the annulation may be difficult to discern, due to their close spacing (~0.2 mm) and low relief on the fossil materials.^[25] Body and appendages are circular in cross-section.^[25]

Lobopod

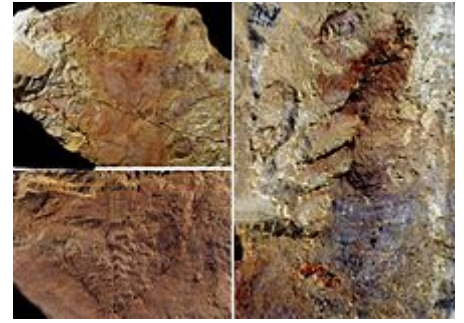
The limbs of lobopodians, technically called lobopods^[4] or lobopodous limbs,^[12] are loosely conical in shape, tapering from the body to their clawed^{[25][15]} or claw-lacking^{[6][26][27][13]} tips. Usually the longest and most robust legs are at the middle of the trunk, with those nearer the anterior and posterior more spindly.^[25] The claws, if present, are slightly curved, and their length is loosely proportional to the length of the leg to which they are attached.^[25] In some genera, the lobopods may bear additional structures such as spines (e.g. *Diania*^[27]), fleshy outgrowths (e.g. *Onychodictyon*), or tubercules (e.g. *Jianshanopodia*^[6]). There's no signs of arthropodization (development of harden exoskeleton and segmental division on panarthropod appendages) in known members of lobopodians even for those belong to the arthropod stem-group (e.g. gilled lobopodians and siberiids), and the suspected case of arthropodization on the limbs of *Diania*^[28] is considered to be a misinterpretation.^{[27][13]}



Diania cactiformis, a lobopodian with unusually robust, spiny, claw-lacking lobopods.

Head

Heads are more or less bulbous,^[4] and may bear a pair of pre-ocular, protocerebral^[18] appendages – for examples primary antennae^{[26][24][18][13]} or well-developed frontal appendages,^{[4][12][29][6]} which are individualized from the trunk lobopods^{[18][30]} (with the exception of *Antennacanthopodia*, which have two pairs of head appendages instead of one^[26]). Mouthparts may consist of rows of teeth^{[25][16][29][6][31]} or conical proboscis.^{[32][4]} The eyes may be represented by one or be numerous^[33] pairs of simple ocelli^[4] as has been shown in *Paucipodia*,^[25] *Luolishania*,^[24] *Miraluolishania*,^[33] *Ovatiovermis*,^[34] *Onychodictyon*,^[32] *Hallucigenia*,^[16] and possibly *Aysheaia* as well.^[32] However in gilled lobopodians like *Kerygmachela*, the eyes are relatively complex reflective patches.^{[35][36]}



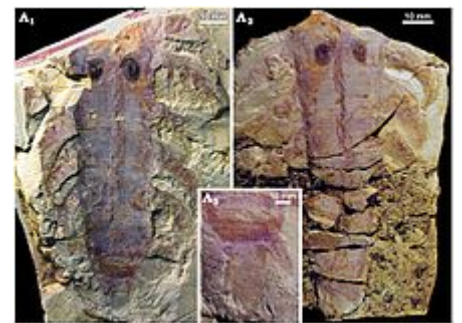
Fossil of *Jianshanopodia decora*, showing head region (upper left) compose of robust frontal appendage (right) and pharynx with rows of teeth (bottom left).

Trunk

The trunk is elongated and compose of numerous body segments (somites) each bore a pair of lobopod, but the segmental boundaries are not externally significant as those of arthropods. The trunk segments may bear other external structures such as turbeclles (e.g. *Hadranax*,^[5] *Kerygmachela*^[12]), spine/plate-like sclerites (e.g. armoured lobopodians^[4]) or flaps (e.g. gilled lobopodians^{[12][31]}). Differentiation between trunk appendages barely occure, except in luolishaniids and hallucigenids, where numerous pairs of their anterior lobopods are significantly slender and/or setose contrast to their posterior counterparts.^{[4][34]} The trunk may terminate with a pair of lobopod (e.g. *Aysheaia*, *Hallucigenia*)^[16] or tail-like extension (e.g. *Siberion*, *Jianshanopodia*).^{[6][37]}

Internal structures

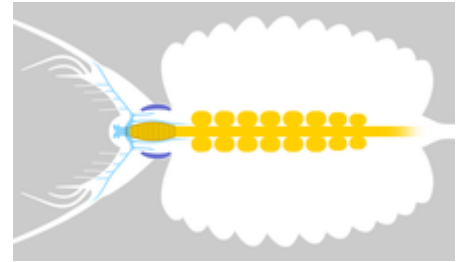
The gut of lobopodians is often straight, undifferentiated,^[38] and sometimes preserved in the fossil record in three dimensions. In some specimens the gut is found to be filled with sediment.^[25] The gut consists of a central tube occupying the full length of the lobopodian's trunk,^[6] which does not change much in width - at least not systematically. However in some groups, specifically the gilled lobopodians and siberiids, the guts were surrounded by pairs of serially repeated kidney-shaped gut diverticulae (digestive glands).^{[6][29][38]} In some specimens, parts of the lobopodian gut can be preserved in three dimensions. This cannot result from phosphatisation, which is usually responsible for 3-D gut preservation,^[39] for the phosphate content of the guts is under 1%; the contents comprise quartz and muscovite.^[25] The gut of the representative *Paucipodia* is variable in width, being widest at the centre of the body. Its position in the body cavity is only loosely fixed, so flexibility is possible.



Fossilized posterior trunk region of *Jianshanopodia decora*, showing traces of lobopods, gut diverculae and lobe-like terminal extension.

No much are known about the neural anatomy of lobopodians due to the spare and mostly ambiguous fossil evidence. Possible traces of brain and ventral nerve cord were found in *Megadictyon* and *Paucipodia*, respectively.^{[29][25]} The first confirmed evidence of lobopodian neural structures comes from the gilled lobopodian *Kerygmachela* in a 2018 study — it presents a brain compose of only protocerebrum (the frontalmost cerebral ganglion of panarthropods) which were directly connect to the nerves of eyes and frontal appendages, suggest the protocerebral ancestry of the head of lobopodians as well as panarthropods.^[35]

In some extant ectdysozoan such as priapulids and onychophorans, there is a layer of outermost circular muscles and a layer of innermost longitudinal muscles. The onychophorans also has a third intermediate layer of interwoven oblique muscles between the two others. But the musculature of a fossil lobopodian Tritonychus show the opposite pattern; it is the outermost muscles that are longitudinal and the innermost layer consisting of circular muscles.^[40]



Eyes (deep blue), brain (light blue) and digestive system (yellow) of *Kerygmachela*.

Categories

Based on external morphology, lobopodians may fall under different categories — for example the general worm-like taxa as "xenusiid" or "xenusian"; xenusiid with sclerite as "armoured lobopodians"; and taxa with both robust frontal appendages and lateral flaps as "gilled lobopodians". Some of them were originally defined under a taxonomic sense (e.g. class Xenusia), but neither any of them are generally accepted as monophyletic in further studies.^{[15][17][18]}

Armoured lobopodians

Armoured lobopodians referred to xenusiid lobopodians which bore repeated sclerites such as spine or plates on their trunk (e.g. *Hallucigenia*, *Microdictyon*, *Luolishania*) or lobopods (e.g. *Diania*). In contrast, lobopodians without sclerites may be referred to as "unarmoured lobopodians".^{[26][13]} Function of the sclerites were interpreted as protective armor and/or muscle attachment points.^{[41][4]} In some cases, only the disarticulated sclerites of the animal were preserved, which represented as component of small shelly fossils (SSF).^[10] Armoured lobopodians were suggest to be onychophoran-related and may even represent a clade in some previous studies,^[41] but their phylogenetic positions in later studies are controversial. (see text)



Fossil of *Microdictyon*, showing pairs of sclerite and trace of trunk and lobopods.



Model of *Microdictyon* at the Chengjiang fossil site museum.

Gilled lobopodians

Gilled lobopodians referred to dinocaridids with lobopodian affinities (e.g. annulation, lobopods) and a pair of flaps on each of their trunk segments, but no signs of arthropodization on their robust frontal appendages like those of a derived dinocaridid taxon: Radiodonta. Gilled lobopodians were recognized by at least two genera: *Pambdelurion* and *Kerygmachela*.^[13] *Opabinia* may also fall under this category in a broader sense,^{[17][42]} although the present of lobopods in this genus are more or less ambiguous.^[43] *Omnidens*, a genus known only by *Pambdelurion*-like mouth apparatuses, may also be a gill lobopodian as well.^[31] The body flaps may function as swimming appendages and/or gills,^[14] and possibly homologous to the dorsal flaps of radiodonts and exopods of euarthropods.^{[12][42]} Gilled lobopodians are not considered lobopodians in some usage,^[44] and they are widely accepted as stem-group arthropods just basal to radiodonts.^{[17][15][16][18]}



The gilled lobopodians *Opabinia* (middle top), *Pambdelurion* (bottom left) and *Kerygmachela* (bottom right).

***Siberion* and similar taxa**

Siberion, *Megadictyon* and *Jianshanopodia* may be grouped taxonomically as Siberiida or siberiids by some studies.^[37] They are generally large (body length ranging between 7^[37] and 22 centimeters^[29]) xenusiid lobopodians with wide trunk, stout trunk lobopods without evidence of claws, and most notably a pair of robust frontal appendages.^[17] With the exception of *Siberion*, they also have digestive glands like those of a gilled lobopodian and basal euarthropod.^{[17][38]} Their anatomy represents transitional forms between typical xenusiids and gilled lobopodians,^[37] eventually placing them under the basalmost position of arthropod stem-group.^{[6][29][17][18]}



The siberiid lobopodians *Siberion* (upper left), *Megadictyon* (bottom center) and *Jianshanopodia* (upper right).

Paleoecology

Lobopodians may have occupied a wide range of ecological niches. Although most of them had undifferentiated appendages and straight gut, which would suggest a simple sediment-feeding lifestyle,^[4] sophisticated digestive glands and large size of gilled lobopodians and siberiids would allow them to consume larger food items,^{[4][38]} and their robust frontal appendages may even suggest a predatory lifestyle.^{[6][38]} On the other hand, luolishaniids such as *Luolishania* and *Ovatiovermis* have elaborate feather-like lobopods that presumably formed 'baskets' for suspension or filter-feeding.^{[24][34]} Lobopods with curved terminal claws may have given some lobopodians the ability to climb on substances.^[4]

Not much is known about the physiology of lobopodians. There is evidence that suggests that lobopodians moult just like other ecdysozoan taxa, but the outline and ornamentation of the hardened sclerite did not vary during ontogeny.^[11] The gill-like structures on the body flaps of gilled lobopodians and ramified extensions on the lobopods of *Jianshanopodia* may provide respiratory function (gills).^{[14][6]} *Pambdelurion* may control the movement of their lobopods in a way similar to onychophorans.^[45]

Distribution

During the Cambrian, lobopodians displayed a substantial degree of biodiversity. One species is known from each of the Ordovician and Silurian periods,^{[8][46]} with a few more known from the Carboniferous (Mazon Creek) — this represents the paucity of exceptional lagerstätten in post-Cambrian deposits.

Phylogeny

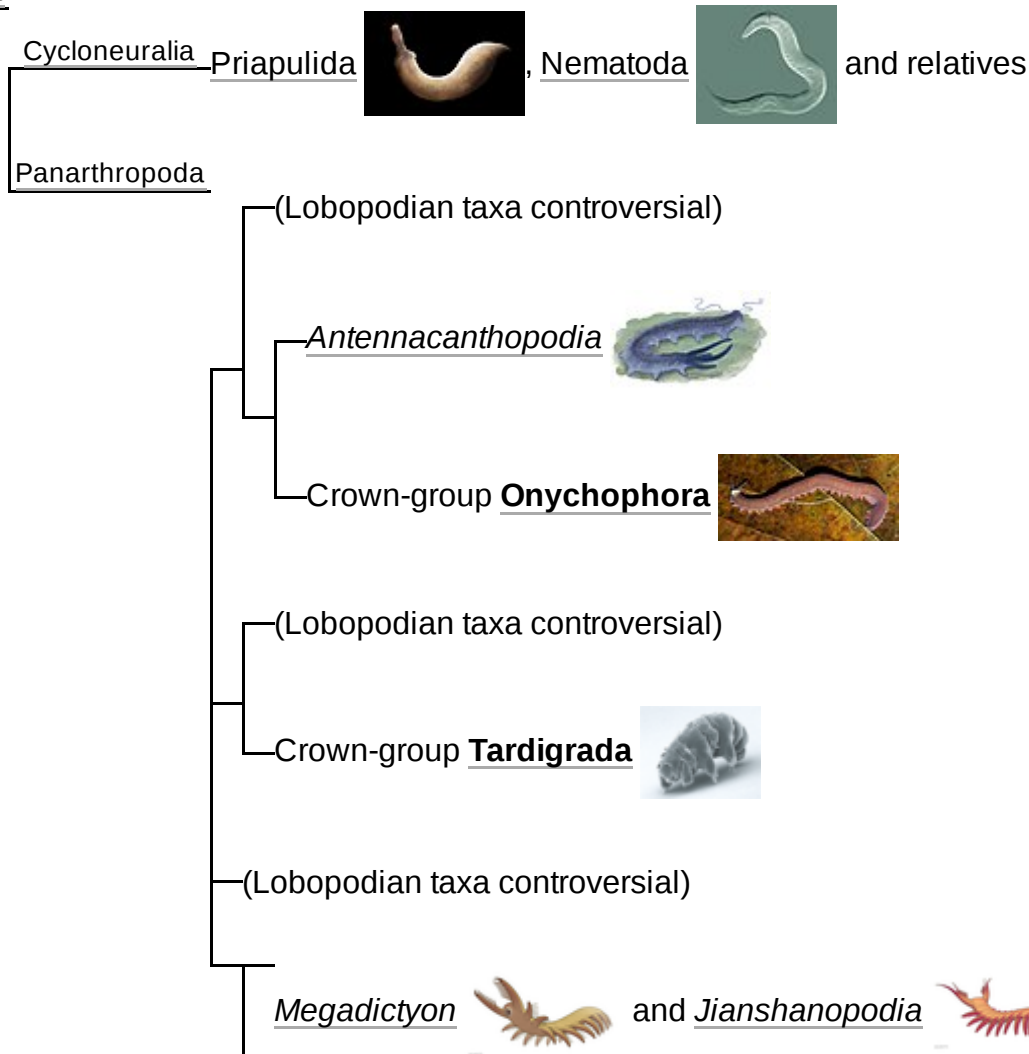
The overall phylogenetic interpretation on lobopodians changed dramatically beyond decades.^[4] The reassignments are not only based on new fossil evidence, but also new embryological, neuroanatomical, and genomic (e.g. gene expression, phylogenomics) informations observed from extant panarthropod taxa.^{[4][18][47]}

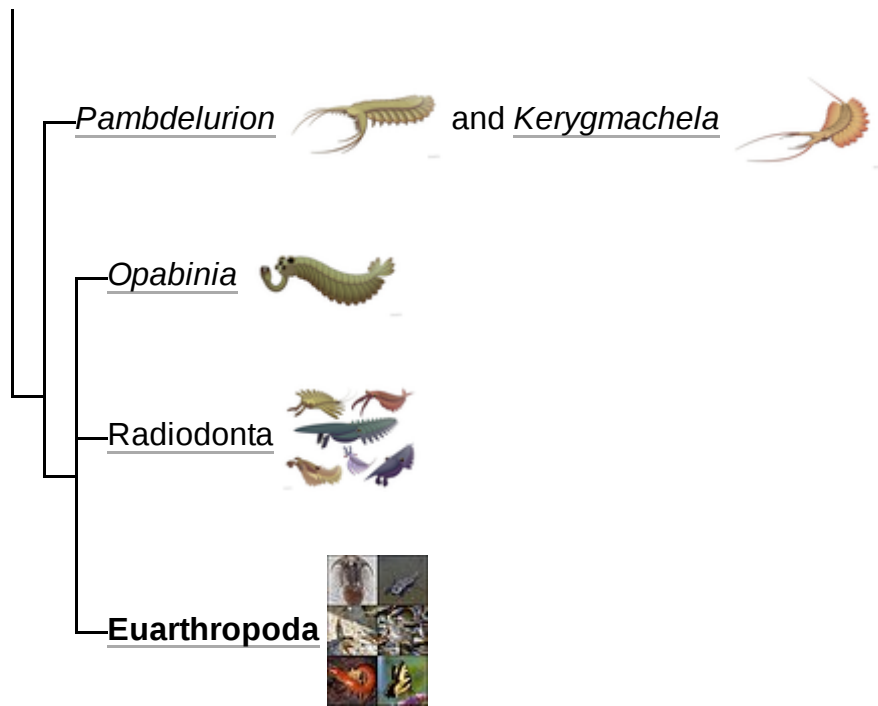
Based on their apparently onychophoran-like morphology (e.g. annulated cuticle, lobopodous appendage with claws), lobopodians were traditionally thought to be present a group of paleozoic onychophorans.^{[4][48][49][50]} This interpretation was flawed after the discovery of lobopodians with arthropod and tardigrade-like characters,^[51] suggest the similarity between lobopodians and onychophorans represent deeper panarthropod ancestral trait (plesiomorphies) instead of onychophoran-exclusive characters (synapomorphies).^[19] For example, The British palaeontologist Graham Budd sees the Lobopodia as representing a basal grade from which the phyla Onychophora and Arthropoda arose, with Aysheaia comparable to the ancestral plan, and with forms like Kerygmachela and Pambdelurion representing a transition that, via dinocaridids to arthropods, would lead to an arthropod body plan.^[41] Aysheaia's surface ornamentation, if homologous with palaeoscolecids sclerites, may represent a deeper link



Reconstruction of a suspension-feeding lobopodian *Ovatovermis cribratus*, showing how it use the anterior 6 pairs of lobopods to gather food particles, while using the posterior 3 pairs of lobopods to anchor itself.^[34]

/SOZoa





alized phylogeny between lobopodians and other Ecdysozoan taxa.^{[15][17][16][42][18][34][19]} Extant panarthropod are in **bold**. Relationship between the total-group of extant panarthropod phyla is unresolve.

connecting it with cycloneuralian outgroups.^[41] Many further studies follow and extend the idea, generally agreed that all three panarthropod phyla have lobopodians in their stem lineages.^{[4][15][16][18][34][19]} Lobopodians are thus paraphyletic, and include the last common ancestor of arthropods, onychophorans and tardigrades.^[4]

As stem-group arthropods

Compared to other panarthropod stem-groups, suggestion on the lobopodian members of arthropod stem-group is relatively consistent — siberiid like Megadictyon and Jianshanopodia occupied the basalmost position, gilled lobopodians Pambdelurion and Kerygmachela branch next, and finally lead to a clade compose of Opabinia, Radiodonta and **Euarthropoda** (crown-group arthropods).^{[15][17][16][42][18][34][19]} Their positions within arthropod stem-group are indicated by numerous arthropod groundplans and intermediate forms (e.g. arthropod-like digestive glands, radiodont-like frontal appendages and dorso-ventral appendicular structures link to arthropod biramus appendages).^{[17][18]} Lobopodian ancestry of arthropods also reinforced by genomic studies on extant taxa — gene expression support the homology between arthropod appendages and onychophoran lobopods, suggests that modern less-segmented arthropodized appendages evolved from annulated lobopodous limbs, with multipodomorous appendages of extinct basal euarthropods (e.g. fuxianhuiids) may represent an intermediate form.^[30] On the other hand, primary antennae and frontal appendages of lobopodians and dinocaridids may be homologous to the labrum/hypostome complex of euarthropods, an idea support by their protocerebral origin^{[17][18][35]} and developmental pattern of the labrum of extant arthropods.^{[30][18]}



Radiodonts are stem-group arthropods with gilled lobopodian-like body flaps, arthropodized frontal appendages and stalked compound eyes.

Fossilized anterior region of a fuxianhuiid arthropod Chengjiangocaris kunmingensis, showing multisegmented appendages which may represent intermediate form between annulated lobopods and modern arthropod appendages.

Diania, a genus of armoured lobopodian with stout and spiny legs, were originally thought to be associated within the arthropod stem-group based on its apparently arthropod-like (arthropodized) trunk appendages.^[28] However, this interpretation is questionable as the data provided by the original description are not consistent with the suspected phylogenetic relationships.^{[52][53]} Further re-examination even revealed that the suspected arthropodization on the legs of *Diania* was a misinterpretation — although the spine may have hardened, the remaining cuticle of *Diania*'s legs were soft (not harden nor sclerotized), lacking any evidence of pivot joint and arthrodial membrane, suggest the legs are lobopods with only widely-spaced annulations.^{[27][13]} Thus, the re-examination eventually reject the evidence of arthropodization (sclerotization, segmentation and articulation) on the appendages as well as the fundamental relationship between *Diania* and arthropods.^{[27][13]}

As stem-group onychophorans

While *Antennacanthopodia* is widely accepted as a member of stem-group onychophoran,^{[15][16][18][34][19]} position of other xenusiid genera that previously though to be onychophoran-related are controversial — in further studies, most of them were either suggest to be stem-group onychophorans^{[4][15][18]} or basal panarthropods,^{[34][19]} with a few species occasionally suggest to be stem-group tardigrades and/or stem-group panarthropods.^{[34][19]} A study in 2014 suggest that *Hallucigenia* are stem-group onychophorans based on their claws, which have overlapped internal structures resemble to those of an extant onychophoran.^[15] This interpretation was questioned by later studies, as the structures may present panarthropod plesiomorphy.^[19]



Antennacanthopodia gracilis, a lobopodian suggested to be a stem-group onychophoran.

As stem-group tardigrades

Lobopodian taxa of tardigrade stem-group is unclear.^[4] *Aysheaia*^{[34][19]} or *Onychodictyon ferox*^{[15][16]} had been suggest to be a possible member. Although not widely accepted, there are even suggestions that Tardigrada itself representing the basalmost panarthropod or branch between the arthropod stem-group.^[51]

As stem-group panarthropods

It is unclear that which lobopodians represent members of the panarthropod stem-group, which were branched just before the last common ancestor of extant panarthropod phyla. *Aysheaia* may have occupied this position based on its apparently basal morphology;^{[41][15][16]} while other studies rather suggest luolishaniid and hallucigenid,^{[34][19]} two lobopodian taxa which had been resolved as members of stem-group onychophorans as well.^{[4][15][18]}

Described genera

As of 2018, over 20 lobopodian genera have been described.^[13] The fossil materials being described as lobopodians *Mureropodia apae* and *Aysheaia prolata* are considered to be disarticulated frontal appendages of the radiodonts *Caryosyntrips* and *Stanleycaris*, respectively.^{[54][55][56]} *Miraluolishania* was suggested to be synonym of *Luolishania* by some authors.^{[57][58]} The enigmatic *Facivermis* was later revealed to be a highly specialized genus of luolishaniid lobopodians.^{[37][34][59]}



Fossil of *Aysheaia pedunculata*.



Fossil of *Microdictyon* sp.



Fossil of "*Mureropodia apae*", which may be in fact frontal appendage of *Caryosyntrips camurus*.

- *Antennacanthopodia*
- *Aysheaia*
- *Carbotubulus*
- *Cardiodictyon*
- *Collinsium*
- *Collinsovermis* ^[60]
- *Diania*
- *Facivermis*
- *Hadranax*
- *Hallucigenia*
- *Jianshanopodia*
- *Kerygmachela*
- *Lenisambulatrix*
- *Luolishania*
- *Megadictyon*
- *Microdictyon*
- *Miraluolishania* (= *Luolishania*?)
- *Onychodictyon*
- *Pambdelurion*
- *Paucipodia*
- *Siberion*
- *Thanahita*
- *Tritonychus*
- *Ovatiovermis*
- *Orstenotubulus*
- *Xenusion*



Reconstruction of *Facivermis*, an unusual lobopodian with limbless posterior region.

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